

Two New Species of Fossil Walruses (Pinnipedia: Odobenidae) from the Upper Pliocene San Diego Formation, California

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ABSTRACT.—Two new species of fossil walruses (Family Odobenidae) from the San Diego Formation (upper Pliocene; Blancan correlative) of San Diego County, California, are referred to the extant Odobeninae and the extinct Dusingathinae. The humerus of the new odobenine taxon shares several apomorphies with the type humerus of *Valenictus* from the late Miocene of southeastern California and is assigned to this formerly problematic genus. *Valenictus chulavistensis*, n. sp., is a tusked walrus closely related to modern *Odobenus* but more derived in possessing an entirely edentulous mandible and lacking all postcanine maxillary teeth. The toothlessness of *V. chulavistensis* is unique among known pinnipeds but parallels the condition seen in modern suction-feeding beaked whales (family Ziphiidae) and the narwhal (*Monodon*). The new dusingathine is assigned to the genus *Dusingathus* primarily because of synapomorphies of the lower jaw. *Dusingathus seftoni*, n. sp., possesses enlarged upper and lower canines and a shortened rostrum. The co-occurrence of these taxa in the San Diego Formation indicates that odobenid diversity in the eastern North Pacific continued to be greater than at present at least into late Pliocene time.

INTRODUCTION

The discovery and description of new species of fossil and living organisms is always an illuminating event, as it supplies new data points in the "history of life." Such discoveries are especially important to researchers attempting to reconstruct the phylogeny of groups as divergent as walruses, whose lack of modern diversity contrasts with their greater fossil diversity (Repenning and Tedford 1977). Not only do these discoveries fill out the taxonomic membership of known branches, they may supply the first evidence of previously unknown but related groups. Moreover, they provide insights into the morphological diversity within a clade and help define the taxonomic distribution of specific character states.

This report describes two new species of fossil walruses (family Odobenidae, *sensu* Repenning and Tedford 1977) from the marine upper Pliocene San Diego Formation of San Diego County, California. The new taxa are assignable to two monophyletic (*sensu* Hennig 1966) lineages of odobenids, one to the extinct Dusingathinae (*sensu* Barnes and Raschke 1990), the other to the Odobeninae (*sensu* Repenning and Tedford 1977), the clade that includes the living arctic walrus, *Odobenus rosmarus*.

This report is part of a more general study of the higher systematic relationships of odobenids (Deméré 1994, this volume) and builds upon the earlier work of Repenning and Tedford (1977). A rapidly improving fossil record for odobenids has contributed much to this study.

GEOLOGY

The majority of the new fossil material reported here was collected from marine sandstones of the San Diego Formation (Deméré 1983; Domning and Deméré 1984) as exposed at various localities in the eastern portion of the city of Chula Vista, southwestern San Diego County, California. The San Diego Formation in this area consists of approximately 50 m of interbedded pebble conglomerates, fine-grained massive sandstones, fine-grained laminated sandstones, and shelly sandstones. This sequence of sedimentary rocks was deposited in shoreface to middle-shelf environments (Deméré 1983).

The San Diego Formation has produced abundant and well-preserved remains of marine invertebrates and vertebrates. The marine invertebrate assemblage includes foraminifers, brachiopods, molluscs, crustaceans, and echinoderms (Hertlein and Grant 1960, 1972). The marine vertebrate assemblage includes sharks and rays, bony fishes, sea birds (Howard 1949, 1958; Chandler 1990), cetaceans (Barnes 1973; Deméré 1986), pinnipeds (Berta and Deméré

1986), and sirenians (Domning and Deméré 1984). Remains of terrestrial mammals have also been collected from this rock unit (Table 1).

The co-occurrence of *Stegomastodon* sp., *Titanotylopus* sp., *Equus* sp., *Platygonus* sp., and *Megalonyx* sp. in the San Diego Formation indicates correlation with the Blancan North American Land Mammal Age (NALMA), late Pliocene. In addition, the associated marine invertebrate assemblage indicates correlation with the "San Joaquin" molluscan stage of Addicott (1972), provincial late Pliocene, estimated to be 2–3 million years old (Deméré 1983).

METHODS AND MATERIALS

The fossil material described in this report is housed at the San Diego Natural History Museum, San Diego, California (SDSNH). Comparisons were made with specimens at other institutions including the Natural History Museum of Los Angeles County, Los Angeles, California (LACM) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Of special note is new undescribed material of *Neotherium mirum* examined at the LACM and undescribed material of *Pontolis magnus* examined at the USNM. Additional specimens cited in this report are housed at the Museum of Paleontology, University of California, Berkeley, California (UCMP); Department of Geological Sciences, University of California, Riverside, California (UCR); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); and Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (IRSNB).

Cranial measurements follow Siversten (1954) and Barnes (1979), mandibular measurements follow Repenning and Tedford (1977), and postcranial measurements follow Kellogg (1931).

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Odobenidae Allen, 1880

Subfamily Odobeninae Mitchell, 1968

Valenictus Mitchell, 1961

Type species.—*Valenictus imperialensis* Mitchell, 1961.

Emended diagnosis.—An odobenine walrus distinguished from other taxa by the following apomorphies of the humerus: greatly

enlarged entepicondyle, short and robust shaft, large lesser tuberosity, and narrow bicapital groove.

Distribution.—Late Miocene to late Pliocene of southern and central California.

Included species.—*V. imperialensis* Mitchell, 1961; *V. chulavistensis*, n. sp.

Valenicus chulavistensis n. sp.

Figures 1–7

Diagnosis.—A species of *Valenicus* distinguished from *V. imperialensis* by the following features of the humerus: larger overall size, more sigmoidal posterior profile, sharply keeled supinator ridge, more robust and rectangular entepicondyle, and more obtuse angle between the shaft and the axis of the distal trochlea. Also diagnosed by the following autapomorphies: edentulous dentary, edentulous premaxilla and postcanine maxilla, osteosclerotic long bones, astragalus with broad sulcus calcanei, very reduced collum tali, and coalesced navicular and sustentacular facet. Shares the following apomorphies with tusked odobenines: enlarged, ever-growing upper canines with three layers (globular orthodontine, orthodontine, and cementum), palate narrow and arched longitudinally as well as transversely, enlarged mastoid processes as widest part of skull, shortened temporal fossa with blunt zygomatic arches, and dorsoventrally expanded postorbital process of jugal.

Type material.—Holotype: SDSNH 36786, a partial skeleton preserving the left side of the skull (maxilla, jugal, squamosal, mastoid, occipital condyle), nearly complete mandible, partial vertebral column (5 cervical, 12 thoracic, 2 lumbar, 4 sacral, and 5 caudal vertebrae), partial right and left scapulae, left humerus, radius, ulna, and manus, partial right manus, left femur, right pes, and partial left pes. Collected by Richard A. Cerutti.

Paratype: SDSNH 38227, a nearly complete skull with both canines but lacking the nasals, premaxillae, and middle ear ossicles. Collected by Richard A. Cerutti.

Etymology.—The specific name is for the city of Chula Vista, San Diego County, California, where the remains of this, and many other Pliocene marine mammals, have been found.

Holotype and paratype locality.—SDSNH locality 3551, Rancho Del Rey, city of Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, "lower member" (Deméré 1983); late Pliocene (Blancan NALMA correlative).

Referred material.—The following SDSNH specimens were all collected from the San Diego Formation (complete locality information is available to interested researchers upon request): 38228, partial rostrum preserving the left maxilla and premaxilla; 15162, partial left C¹; 38225, right C¹; 38226, partial right C¹; 35284, partial left C¹; 25180, partial right C¹; 30796, fragmentary right C¹; 35276, partial atlas vertebrae; 36796, fused sacral vertebrae (3); 38676, fused sacral vertebrae (3); 38394, left scapula; 38308, partial left humerus; 38307, right humerus, distal end; 38286, left humerus, distal end; 35263, partial left humerus; 38315, left humerus; 35275, right humerus; 38312, left humerus; 38300, partial left humerus; 38230, right ulna; 32790, right radius; 38288, left radius; 38324, right radius; 38650, right radius; 36799, left scapularium; 36800, left unciform; 38201, left magnum; 38208, left metacarpal I; 42694, left metacarpal I; 38206, left metacarpal IV; 38339, associated right and left innominate and partial baculum; 38310, left innominate; 25145, partial left innominate; 38291, partial right innominate; 38325, partial left innominate; 32770, fragmentary right innominate; 36798, right innominate; 42751, partial left hindlimb with femur, tibia, fibula, calcaneum, navicular, mesocuneiform, and metatarsals I, II, and III; 25394, left femur; 25074, left femur; 25076, left femur, distal end; 42690, right femur; 38245, right femur, proximal end; 32767, left femur, distal end;

32777, left fibula, distal end; 42654, right fibula; 42655, right fibula; 22290, right tibia; 25087, left tibia, distal end; 35296, right tibia, distal end; 33935, left tibia, distal end; 38633, partial left tibia; 35273, left astragalus; 21130, right calcaneum; 22412, right calcaneum; 32765, left calcaneum; 25179, associated ribs and hindlimb bones with right patella and navicular, and left entocuneiform and metatarsal II; 38209, left metatarsal I; 38261, left metatarsal I.

Cranium.—The holotype partial skull (SDSNH 36786) is from a mature adult male, as indicated by closure of all preserved sutures and the narrowing of the proximal end of the upper canine (Rutten 1907).

In contrast, the paratype skull (SDSNH 38227, Figs. 1A, B; 2A, B) is from an immature male (F. H. Fay, pers. comm.). The tusks in this skull taper continuously from the root to the distal end, and many sutures are distinct. This skull was shortened anteroposteriorly by lithostatic load, with the palate displaced against the auditory bullae and beneath the basioccipital. Portions of the zygomatic arches and braincase were partially etched by root action and soil acidity. The premaxillae were largely destroyed by a bulldozer at the time of their discovery.

A referred left rostral fragment (SDSNH 38228, Figs. 2C, D) is from an immature female (F. H. Fay, pers. comm.) and of the three cranial specimens preserves the smallest canine alveolus (Table 2). The maxillary portion of SDSNH 38228 is nearly complete (surfaces are preserved for the maxilla/jugal, maxilla/frontal, maxilla/palatine, and maxilla/nasal sutures) and occurred with the only premaxilla known for this taxon.

The cranium of *V. chulavistensis* preserves many features characteristic of the tusked odobenines, including a narrow longitudinally and transversely arched palate (as in *Odobenus rosmarus* and *Alachtherium cretsii*), mastoid processes as the widest part of the skull, diagonally oriented orbitosphenoid with small, funnel-shaped optic foramen, lack of a sagittal crest, telescoping of palate beneath anterior portion of basicranium, and posterior elongation of the hard palate to the level of the glenoid fossae. In addition, the skull of this new species also preserves more generalized odobened features including lack of supraorbital processes and large antorbital processes constructed from both maxilla and frontal.

In lateral aspect the premaxilla of SDSNH 38228 is shaped roughly like an acute right triangle, the hypotenuse being the external narial border. Anteriorly the premaxillae terminate in a conspicuous nasal process, as in *Zalophus californicus* (see Howell 1929) and most fossil odobenines (e.g., *Neotherium mirum* and *Imagotaria downsii*). The nasal process is elevated above the canine alveolus as in *Odobenus* and *Alachtherium*; however, the vertical dimension between the nasal process and the incisive border of the premaxilla is short. In *Odobenus* the nasal process is very reduced (in adults) and the narial opening is elevated well above the incisive margin. The incisive region of the premaxilla in the new taxon is edentulous, lacking all traces of alveoli (Figs. 1B, 2C). The incisive foramina are distinct and oriented nearly horizontally as they extend posterodorsally into the narial opening. The external narial opening in SDSNH 38228 would have been a transversely compressed oval, measuring approximately 38 mm high by 29 mm wide. In lateral aspect the narial opening makes an angle of approximately 40° with the horizontal axis of the skull. In *Odobenus* this angle is approximately 70° and in *Alachtherium* approximately 55°.

Unlike the derived condition in *Odobenus*, the ascending processes of the premaxillae of *Valenicus chulavistensis* overlapped the nasal bones externally for approximately one-half the length of the nasals. This assessment is based on the configuration of the sutures, as the nasals themselves are not preserved.

The maxillae of all three rostral specimens are conspicuously swollen in the region of the canine root (Fig. 3). However, this

TABLE 1. Composite faunal list of mammals from the San Diego Formation.

Rodentia
Heteromyidae
Heteromyidae sp.
Cricetidae
<i>Neotoma</i> sp.
Lagomorpha
Leporidae
Leporidae sp.
Artiodactyla
Tayassuidae
<i>Platygonus</i> sp.
Camelidae
<i>Titanotylopus</i> sp.
cf. <i>Hemiauchenia</i> sp.
Cervidae
Cervidae sp.
Perissodactyla
Equidae
<i>Equus</i> sp.
Tapiridae
<i>Tapirus</i> sp.
Carnivora
Felidae
<i>Felis</i> sp. cf. <i>F. rexroadensis</i>
Mustelidae
<i>Spilogale</i> sp.
Canidae
Caninae sp.
Otiariidae
<i>Callorhinus gilmorei</i> Berta and Deméré
Otiariidae sp.
Odobenidae
<i>Valenictus chulavistensis</i> n. sp.
<i>Dusignathus seftoni</i> n. sp.
Cetacea
Mysticeti
"Cetotheriidae"
<i>Herpetocetus</i> sp. 1
<i>Herpetocetus</i> sp. 2
Balaenopteridae
<i>Balaenoptera davidsonii</i> Cope
Balaenopteridae sp. 1
Balaenopteridae sp. 2
Balaenopteridae sp. 3
Balaenopteridae sp. 4
Balaenidae
Balaenidae sp. 1
Balaenidae sp. 2
Odontoceti
Pontoporiidae
<i>Parapontoporia sternbergi</i> Gregory and Berry
Phocoenidae
Phocoenidae sp. 1
Phocoenidae sp. 2
Monodontidae
Delphinapterinae sp.
Delphinidae
Delphinidae sp. 1
Delphinidae sp. 2
Sirenia
Dugongidae
<i>Hydrodamalis cuetiae</i> Domning
Proboscidea
Gomphotheriidae
<i>Siegmastodon</i> sp.
Edentata
Megalonychidae
<i>Megalonyx</i> sp.

swelling is not as great as in *Odobenus* and is expressed more anteroposteriorly than transversely. In *Odobenus*, the maxillae are so swollen that the infraorbital foramina are almost completely hidden when the skull is viewed in anterior aspect. The inclination of the canine root in relation to a vertical transverse plane (Fay 1982:111) is more procumbent (Fig. 2B) than that of *Odobenus* (36° – 56° in *V. chulavistensis*, compared with 9° – 20° in *Odobenus*, and 25° – 48° in *Alachtherium*). As in all pinnipeds, the maxillae form the anterior walls of the orbits (Wyss 1987). The infraorbital foramen is large (19 mm wide by 33 mm high in SDSNH 38227; 12 by 28 mm in SDSNH 36786; 19 by 20 mm in SDSNH 38228), with a delicate dorsal strut and more robust ventral strut. The ventral surface of the latter is marked by a conspicuous fossa, which opens posteroverntally to accommodate the sharply keeled dorsal margin of the dentary. The ventral margin of the maxilla, posterior to the large canine alveolus, is keeled between the lateral and palatal surfaces, and is continuous with the lateral keeled margin of the ventral strut of the infraorbital foramen (Fig. 3). In lateral aspect, the ventral margin of the maxilla in *Odobenus* is continuous lingually with an alveolar shelf, and is continuous labially with the ventral strut of the infraorbital foramen as in *V. chulavistensis*. This is unlike the condition in *Neotherium*, *Imagotaria*, *Pontolis*, *Dusignathus*, *Aivukus*, and *Gomphotaria*, in which the ventral strut of the infraorbital foramen is conspicuously elevated above the ventral (alveolar) margin of the maxilla.

The jugal is relatively longer and more transversely compressed in *V. chulavistensis* than in *Odobenus*. However, as in *Odobenus*, the jugal in the new species contacts the maxilla in a transversely compressed peg-and-socket joint. The postorbital process of the jugal of *V. chulavistensis* is large and dorsoventrally expanded as in *Odobenus*. The orbit (i.e., diameter between the maxillary border of the orbit and the postorbital process of the jugal) is small as in *Odobenus*, relatively smaller than in *Aivukus*, *Pontolis*, *Imagotaria*, and *Neotherium*.

The zygomatic portion of the squamosal is robust and shortened as in *Odobenus* and *Alachtherium*, not slender and elongated as in all other fossil odobenids (including *Aivukus*). The squamosal fossa at the root of the zygoma is short and narrow and continuous posteriorly with a narrow shelf above the external auditory meatus. The external auditory meatus is open broadly externally and not restricted by the closeness of the mastoid and postglenoid processes, as it is in adult crania of *Odobenus*.

In dorsal aspect, the temporal fossae are oval openings antero-posteriorly shortened relative to those of *Neotherium*, *Imagotaria*, *Gomphotaria*, and *Aivukus*. They are not as shortened, however, as those of *Odobenus*.

The squamosal/parietal suture is horizontal and positioned near the base of the broadly convex braincase. The cranial vertex is broadly rounded transversely (as in *Odobenus*) and marked by a weakly raised interparietal suture. There is no indication of the sagittal sulcus described by Ruten (1907) for the holotype cranial fragment of *Alachtherium antverpiensis* (= *A. cretsii*), nor of the parasagittal cristae seen on adult crania of *Odobenus*.

The parietal/frontal suture is partially preserved on the right side of SDSNH 38227 at the level of the intertemporal constriction. The suture indicates that the frontals extended posteriorly between the parietals at the midline, as in *Odobenus*. Anterior to the intertemporal constriction the frontals widen dramatically, terminating anterolaterally in large antorbital processes. The frontal/maxilla suture is obscure but seems to have been transversely oriented. It is clear, however, that the suture bifurcates the antorbital processes, so both maxilla and frontal form the processes.

Near the midline, the lambdoidal crest is developed medially as a distinctive, anterodorsally inclined, transverse crescentic shelf (convex border anteriorly placed) that joins with its more lateral

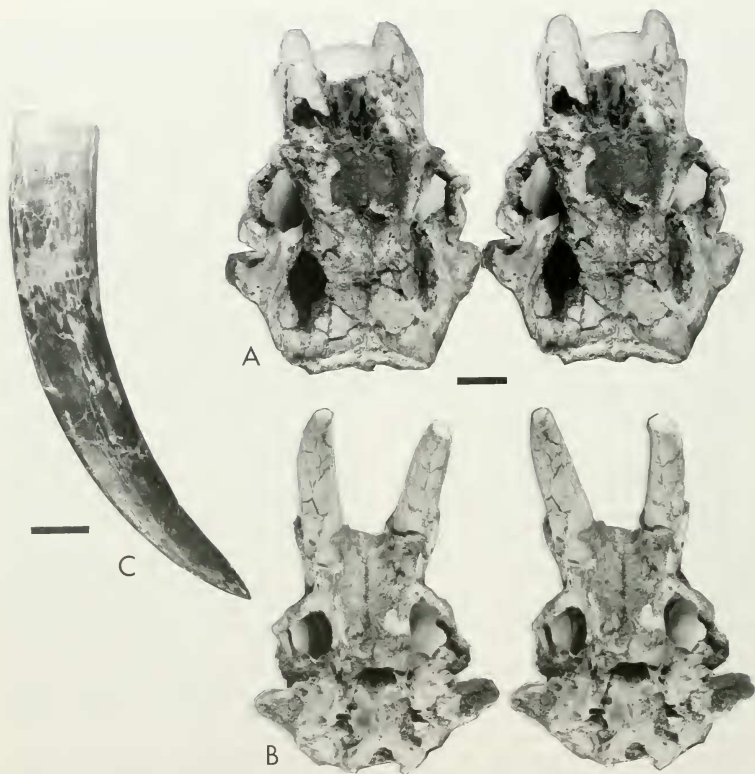


Figure 1. *Valenictus chulavistensis*, new species. A, B, SDSNH 38227, paratype skull. A, dorsal view (stereophotographs); B, ventral view (stereophotographs). C, SDSNH 38225, referred right C¹, medial view. Scale bar, 5 cm.

portions as they descend toward the mastoid processes. This inclined shelllike crest (the site of insertion of neck extensor muscles) is also seen in *Odobenus*, the holotype of *Alachtherium antverpiensis* (Rutten, 1907), the holotype of *Alachtherium antverpiensis* Hasse, 1910, and the referred skull of *Alachtherium antverpiensis* (Rutten 1907) described by Erdbrink and van Bree (1990). The lambdoidal crest does not project posterodorsally to overhang the occipital shield as in *Neotherium*, *Imagotaria*, *Pontolis*, and *Gomphotaria*. The occipital shield is vertically oriented with a distinct sagittal crista as in *Odobenus* and *Alachtherium*. In posterior aspect (Fig. 2A) the occiput is hemispherical as in *Odobenus* and differs from the

rectangular shield characteristic of *Alachtherium* (see Hasse 1910). The occipital condyles are widely separated dorsally, do not reach the roof of the foramen magnum, and are not exceptionally large.

The basioccipital is broad and roughly pentagonal (Figs. 1B; 3). The posterior portion of the basioccipital bears a strong sagittal ridge, bounded anterolaterally on either side by rugose circular areas for insertion of the rectus capitis ventralis muscles. A portion of the basioccipital/basisphenoid suture is preserved at the anterolateral corners of the basioccipital.

The auditory bulla completely fills the portion of the basiocranium between the basioccipital, mastoid, and postglenoid pro-

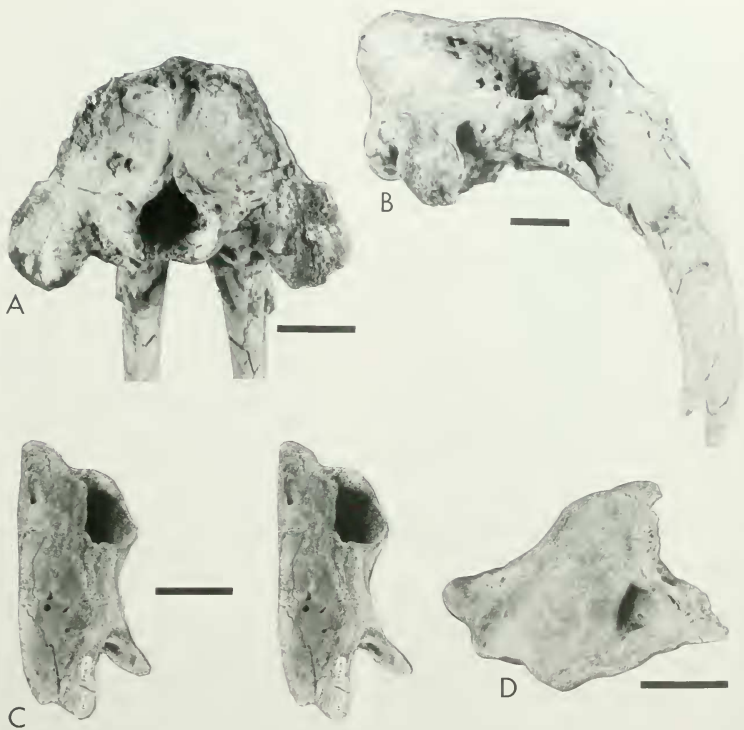


Figure 2. *Valenictus chulavistensis*, new species. A, B, SDSNH 38227, paratype skull. A, posterior view; B, lateral view. C, D, SDSNH 38228, referred left maxilla and premaxilla. C, ventral view (stereophotographs); D, lateral view. Scale bar, 5 cm.

cess. The bulla is not inflated except near the posterior opening of the carotid canal. This opening is rather steeply inclined anterodorsally as in adult crania of *Odobenus* and is closely appressed to a small posterior lacerate foramen. There is no clear distinction between the entotympanic and ectotympanic. Anteriorly, the bulla is closely appressed to, and overrides, the posterior portion of the postglenoid process. Several distinct and irregular bullar processes lie anterior to the hyoid fossa and stylo mastoid foramen. The latter foramen is a large cylindrical opening well separated from the large, slitlike hyoid fossa by a smooth continuous surface extending from the bulla laterally out onto the ventromedial surface of the mastoid process. This condition is like that in *Odobenus* and *Alachtherium* and unlike that in *Imagotaria* and *Pontolis*, in which the two openings are connected by a continuous

groove, or *Neotherium*, in which the two openings lie very close to one another.

The foramen ovale and alisphenoid foramen are closely appressed and recessed in a common fossa, which is directed ventrally as in *Odobenus*. The anterior opening of the carotid canal and bony eustachian tube are obscured by the diagenetically telescoped basicranium.

The palate is narrow and arched both longitudinally and transversely (Figs. 1B, 2C) as in *Odobenus*. There is no alveolar shelf along the lingual border of the upper canines, as the entire postcanine portion of the maxilla is edentulous, without any trace of alveoli. The maxilla/palatine suture on the palate meets the margin of the temporal fossa at the apex of a small but distinct pterygoid process. Together the horizontal laminae of the palatine bones form

TABLE 2. Skull measurements of *Valenictus chulavistensis* and *Dusignathus seftoni* (in mm).

	<i>Valenictus chulavistensis</i>			<i>Dusignathus seftoni</i>
	SDSNH 36786 ^e	SDSNH 38227 ^b	SDSNH 38228	SDSNH 38342 ^a
Total length (condylobasal length) (0) ^f	410 ^d	222 ^d		320
Rostral tip to middle of occipital crest				83
Length of tooth row, P ¹ -M ²				140 ^e
Width of rostrum across canines (12)	152 ^e	146	112 ^e	56
Width of rostrum across base of I ³				94 ^e
Width of palate at P ⁴				
Depth of greatest palatal arch		56	45	
Width across antorbital processes (5)		147 ^d	116 ^e	108 ^e
Width between infraorbital foramina		127	96 ^e	118 ^e
Width across intertemporal constriction			82	51
Width of braincase (8)				106
Zygomatic width (17)	232 ^e	206		222 ^d
Auditory width (19)		171		
Mastoid width (20)	306 ^e	247		
Paroccipital width		154		
Greatest width across occipital condyles	110 ^e	95		
Greatest width of anterior nares (3)		46 ^d	30 ^e	50
Greatest height of anterior nares			36 ^e	52
Greatest width of nasals			26 ^e	40
Greatest length of nasals (4)				73
Width of zygomatic root of maxilla (14)	38	29	21	21
Greatest width of foramen magnum	42 ^e	48		
Transverse diameter of infraorbital foramen	26	29	23	28

^aHolotype.^bParatype.^cNumbers in parentheses refer to measurements in Siversten (1954).^dEstimate based on bilaterally symmetrical feature.^eEstimate on broken features.

a broad trapezoid, the longest side represented by the internal narial opening and the palatine/pterygoid sutures. The hamular processes of the pterygoids are constructed as in *Odobenus* (i.e., dorsoventrally compressed and transversely expanded flanges that hook laterally at their flattened distal extremities) and are unlike the delicate transversely compressed processes of *Imagotaria*. The medial wall of the pterygoid is preserved within the narial passage, with a clearly defined pterygoid/basisphenoid suture. The hard palate is elongated, extending to the postglenoid fossae as in *Odobenus* and *Alachtherium*, and lacks any hint of the horizontal pterygoid strut (Barnes 1989) that characterizes the lateral borders of the internal narial opening in almost all other pinnipeds. In this configuration the site for origination of the internal pterygoid muscle is moved to the temporal fossa.

The mastoid processes are greatly enlarged, constructed internally from cancellous bone, and extend ventrally to a level below the hamular processes and auditory bullae, as in *Alachtherium* and *Odobenus*. In lateral aspect, the mastoid process presents a broad "teardrop" form that is more convex posterolaterally than in *Odobenus*. The ventral portion of the mastoid is slender and antero-posteriorly compressed to produce a transversely elongate process. In *Odobenus*, the ventral portion of the mastoid is more of a swollen knob, with a conspicuously roughened area for origination of the digastricus muscle. In *V. chulavistensis* the mastoid and paramastoid processes are closely appressed, with the latter forming the thin, delicate process characteristic of odobenids. As in *Odobenus*, the mastoid/paramastoid suture is not fused.

The right orbital wall of SDSNH 38227, although damaged, provides details on the structure of this region. The optic foramen is funnel-shaped and positioned dorsally within a diagonally oriented orbitosphenoid that lacks a conspicuous horizontal plate of bone anterior to the foramen. This unusual configuration is also seen in *Odobenus*. In other pinnipeds, the optic foramen is typically a vertical slot positioned ventrally within a horizontally oriented orbitosphenoid that has a relatively long plate of bone anterior to the foramen. As in *Odobenus*, the orbitosphenoid in *V. chulavistensis* appears to be bounded anteriorly by a relatively large and posteriorly placed orbital vacuity unlike the more anteriorly placed vacuities seen in extant otariids and at least one fossil odobenid (*Imagotaria* sp., USNM 335599). In *Odobenus* the palatine bone forms the entire ventral border of the orbital vacuity, including both the anteroventral and posteroventral portions (i.e., the maxilla/palatine suture meets the maxilla/frontal suture anterior to the vacuity). In otariids (e.g., *Zalophus*, *Eumetopias*, and *Otaria*) and at least one fossil odobenid (*Imagotaria* sp., USNM 335599) the anteroventral border of the vacuity is formed from the maxilla (i.e., the maxilla/palatine suture does not reach to the maxilla/frontal suture but instead contacts the vacuity directly).

A portion of the left petrosal was recovered with SDSNH 38227 and is odobenidlike in its relatively large size, enlarged apex anterior to the promontorium, and broad internal auditory meatus. This meatus has passages for the facial and vestibulocochlear nerves separated by a low transverse crest. The roof of the meatus is not preserved, and much of the promontorium and all of the cochlea

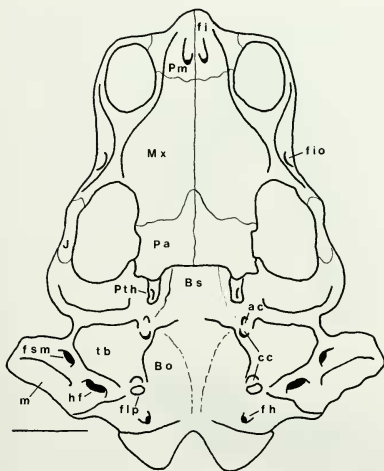


Figure 3. Reconstruction of *Valenictus chulavistensis*, new species, ventral aspect. Based largely on SDSNH 38227. ac, alisphenoid canal; Bo, basioccipital; Bs, basisphenoid; cc, carotid canal; fh, hypoglossal foramen; fi, incisive foramen; fio, infraorbital foramen; flp, posterior lacrate foramen; fsm, stylomastoid foramen; hf, yoid fossa; J, jugal; m, mastoid; Mx, maxilla; Pa, palatine; Pth, hamular process of pterygoid; Pm, premaxilla; tb, tympanic bulla. Scale bar, 5 cm.

and floccular fossa are missing. Thus the fenestra ovale can not be measured. The petrosal apex is anteriorly elongated as in *Aivikus* and not shortened as in *Odobenus*.

Dentition.—The dentition of *Valenictus chulavistensis* consists solely of the upper canines, which are elongated, curved, ever-growing tusks constructed as in *Odobenus rosmarus* and *O. huxleyi* (see Ray 1960). Internally, the tusks of *Odobenus* and *V. chulavistensis* consist of three layers, a central column of globular orthodontine, a surrounding ring of dense compact orthodontine, and a thin outer layer of cementum (Ray 1960). The thicknesses of these layers as measured on a referred partial tusk (SDSNH 38226) are 7.6, 8.9, and 1.5 mm, respectively, for the globular orthodontine (radius), compact orthodontine, and cementum (see Table 3 for additional measurements). This specimen has a bluntly rounded crown and well-worn anterior border. The cementum layer is well preserved proximally and thins toward the anterodistal edge, probably because of wear. The medial surface has two broad longitudinal grooves, the more anterior being more prominent and extending nearly to the distal tip of the tooth. The lateral surface is faintly fluted, with one particularly strong longitudinal groove near the posterior margin. The cementum layer is completely worn away on the tip of the crown and in a longitudinal band running proximally along the anterior margin from the tip back toward the proximal end, where the wear band rolls medially. In a few places where the cementum layer has been broken away, a pattern of very fine

transverse lines (growth lines) is preserved in the compact orthodontine layer, as noted by Ray (1960) for *O. huxleyi*.

SDSNH 38225 is a beautifully preserved complete right canine (Fig. 1C). In contrast to the broadly rounded anterior margin of SDSNH 38226, this specimen has a sharply beveled margin (averaging about 10 mm wide) extending from the distal end 235 mm up the anterior circumference of the tooth. Another beveled surface occurs along the distolateral surface from the tip proximally for a distance of 162 mm. Preserved along the medial border of the anterior half of the tooth, a conspicuous wear surface is bounded by cementum on its margins but lacks cementum itself. This large wear surface is irregularly concave proximally and distally. An intact cementum layer is preserved along the entire posterior margin of the tusk. The intralveolar portion of the tusk is characterized by numerous closely spaced fine longitudinal grooves that terminate abruptly distal to where they encounter the extralveolar surface. This specimen does not preserve any of the broad longitudinal grooves on its medial surface as seen in SDSNH 38226. A faint groove, however, is preserved on the lateral surface within 20 mm of the anterior margin. A second, more conspicuous longitudinal groove occurs just lateral to the posterior margin but does not continue onto the extralveolar surface. On this tusk, cementum is preserved only on the proximalateral surface, the posterior margin, and the distomedial surface. These wear patterns (i.e., abraded and worn anterior surfaces at the distal ends of the crowns) are similar to those reported by Fay (1982) for tusks of *O. rosmarus*. The wear on the distal end of SDSNH 38225 is so extensive that the dense orthodontine layer has been abraded away on the anterior surface to reveal the central globular orthodontine core (a condition also seen in tusks of *O. rosmarus*). The medial surfaces of the tusks of *V. chulavistensis* have broad longitudinal grooves as in *Odobenus* and in contrast to the more numerous and distinct longitudinal grooves preserved on the fluted tusks of *Gomphotaria pugnax* (see Barnes and Raschke 1991).

The tusks in the paratype skull (Fig. 2B) as well as in two nearly complete referred tusks (SDSNH 38225, 38228) are arched in the parasagittal plane (Table 3), as in *Odobenus*. Radii of this arc as measured along the posterior surface of the two referred tusks are 403 and 398 mm, respectively; in a fossil tusk of *O. rosmarus*, 270 mm (Rutten 1907). Fay (1982:111) noted that in living walrus the radius of the longitudinal arc is variable, with ranges of 456 to >5000 mm for males and 226 to 1425 mm for females. The fossil tusks from Chula Vista fall within these ranges and point out the taxonomic weakness of this feature as discussed by Erdbrink and van Bre (1990).

Mandible.—A nearly complete mandible (Fig. 4) was collected with the holotype skeleton (SDSNH 36786) and consists of a left mandibular ramus (lacking only the coronoid process) strongly fused at the symphysis to a partial right horizontal ramus (Table 4). In lateral aspect, the mandible presents a slender profile unlike that of any known pinniped. A slender and strongly upturned symphyseal region forms an angle between the anterior margin and the ventral margin of the horizontal ramus of about 125°. The posterior margin of the upturned symphysis forms an angle of about 130° with the ventral margin. In *Alachtherium* (IRSNB M.170) the symphyseal portion is also upturned but more massive, with the anterior margin of the symphysis forming an angle of only about 112° with the ventral margin and about 143° with the posterior (alveolar) margin.

The ascending, symphyseal portion of the mandible (right and left rami) of *V. chulavistensis* is slender and triangular in cross section (not swollen and massive as in *Odobenus*), with the apex of the triangle corresponding to the anteroventral margin of the symphysis. In *Alachtherium* the ascending symphyseal portion of the mandible is also somewhat triangular. The "incisive" border of the

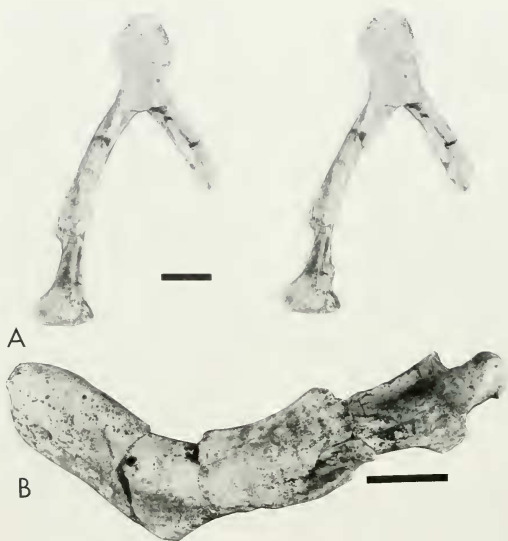


Figure 4. *Valenictus chulavistensis*, new species, SDSNH 36786, holotype mandible. A, dorsal view (stereophotographs); B, lateral view. Scale bar, 5 cm.

mandible is characterized by a highly vascularized, laterally expanded bony pad (as in *Prorosmarus* and *Odobenus*). This bony pad is continuous posteriorly with a broad trough that runs posteroventrally to the point of divergence between the right and left rami. The ridges that form the dorsolateral borders of this symphyseal trough run down and out onto the horizontal rami to become the sharply keeled dorsal margins of the rami. Both rami are entirely edentulous, with no trace of alveoli or alveolar shelves. The horizontal rami are transversely compressed and dorsoventrally shallow (Table 4), in contrast to the deep rami of *Alachtherium*.

On the lateral surface of the horizontal ramus, at the point of divergence of the rami, are a pair of opposing mental foramina, one opening posteriorly, the other anteriorly. Both are set in a deeply excavated and elongated oval fossa. *Alachtherium* possesses a similar pair of mental foramina within an open oval fossa. In *Prorosmarus* and *Odobenus* a single nearly circular mental foramen penetrates deeply into the ramus. At the back of this foramen are a pair of opposing smaller foramina. A pair (right and left) of large longitudinal nutrient foramina lie at the extreme anterior tip of the mandible, just below the bony pad. Similar foramina are seen on the mandibles of *Prorosmarus*, *Alachtherium*, and *Odobenus*.

In lateral aspect, the ventral margin of the ramus between the rugose inferior genial tuberosity and the marginal process is concave. The marginal process (Davis 1964) is well developed and divisible into dorsal and ventral components. The ventral portion of the process is a keeled ridge, set off from the ventral margin of the ramus as a posteriorly directed pointed process. In ventral aspect, the axis of this process diverges medially from that of the ramus. The dorsal portion of the marginal process lies immediately above the posterior end of the ventral portion and is a conspicuous, anteroposteriorly elongated, knoblike eminence. The two portions of the marginal process are separated by an anteroposteriorly oriented sulcus. Dentaries of mature individuals of *Otaria byronia* display a similar divided marginal process (personal observation), while dentaries of immature individuals of *Otaria* display intermediate conditions, from a single conspicuous flangelike marginal process to one that shows incipient division. *Prorosmarus*, *Alachtherium*, and *Odobenus* also possess well-developed marginal processes, although without any obvious division into dorsal and ventral components. The structure of the marginal process in *V. chulavistensis* suggests a large digastric muscle with an anteriorly placed insertion on the ramus. The horizontal ramus is widest at the level of the marginal process.

TABLE 3. Measurements of upper canines (tusks) of *Valenictus chulavistensis* (in mm).

	SDSNH 36786 ^a	SDSNH 38225	SDSNH 38226	SDSNH 38227 ^b
Radius of curvature, anterior surface	265	355	351	
Radius of curvature, posterior surface	312	403	520	
Total length, arc of anterior surface		485		340 ^c
Total length arc of posterior surface		419		320 ^c
Length, tangent of arc of posterior surface		405		311 ^c
Length, base of root to intra-alveolar margin	136	145		125 ^c
Anteroposterior diameter, base of root	74	71		64
Transverse diameter, base of root	36	44		34
Anteroposterior diameter, intra-alveolar margin	81	69		53–54
Transverse diameter, intra-alveolar margin	49	47		36–39
Anteroposterior diameter, mid-crown	68	64		49–49
Transverse diameter, mid-crown	45	42		31–33

^aHolotype.^bParatype (two tusks).^cEstimate on broken feature.

The pterygoid process is large and robust, ventromedially directed, hooklike, and well separated from the marginal process. In *Alachtherium* and *Odobenus* the two processes are positioned close together, with the pterygoid process as a low, anteroposteriorly elongated knoblike projection closely appressed to the ramus and not medially extended.

The mandibular condyle is a robust and transversely elongated cylinder, similar in size and thickness to that of an *Odobenus* of comparable size. The coronoid process is not preserved, but its broken base indicates it was slender and anteroposteriorly elongated. In this respect the coronoid process was probably similar in form to that of *Alachtherium cretisi* and quite different from the short, stout, and broad-based coronoid process of *Odobenus*. In dorsal (occlusal) aspect the mandible has a "wish-bone" or furcula shape, with the left mandibular ramus preserving a distinctive sigmoidal outline, laterally concave between the tip of the jaw and the posterior border of the symphysis and laterally convex from there to the posterior border of the condyle. This sigmoidal outline is also characteristic of mandibles of *Alachtherium*, *Prorosmarus*, and *Odobenus* (see Berry and Gregory 1906) and serves to accommodate the greatly enlarged upper canines (tusks).

Postcrania.—The holotype includes all major portions of the

postcranial skeleton except the tibia and innominate. Fortunately, these elements are represented in additional, referred material. It is beyond the scope of this report to describe each of these skeletal elements. The unique morphology of the humerus, calcaneum, and astragalus, however, calls for discussion of these elements.

Humerus.—The current sample includes five complete and five partial humeri (Table 5). The following description focuses primarily on the holotype (Fig. 5).

The humerus of *Valenictus* is striking in its overall stockiness relative to the more slender and elongated humeri of *Odobenus* and *Alachtherium*. Stockiness, expressed as the ratio of proximal width (measured at the widest part of the lesser tuberosity) to total humeral length, is significantly greater ($p > 0.05$) in *Valenictus* than in other odobenids.

In *V. chulavistensis* the humerus is constructed from very dense osteosclerotic bone, as in sirenians. In other marine mammals, it consists of spongy, cancellous bone. This greater bone density also characterizes all other limb bones of the holotype, including carps, tarsals, and metapodials. Interestingly, in contrast to sirenians, osteosclerotic bone does not occur in the axial skeleton (i.e., vertebrae and ribs) of *V. chulavistensis*. The nature of the internal structure of the holotype humerus of *V. imperialensis* is unknown.

TABLE 4. Mandibular measurements of fossil odobenids (in mm).

	<i>Valenictus chulavistensis</i> SDSNH 36786	<i>Alachtherium cretisi</i> IRSNB M.168	<i>Dusignathus seftoni</i> SDSNH 20801	<i>Dusignathus santacruzensis</i> UCMP 27131
Greatest length	310	364	344	215 ^a
Length of tooth row, P ₁₋₄		98	107	72
Depth of horizontal ramus at P ₂		117	76	64
Width of horizontal ramus at P ₂		30	39	17
Depth of horizontal ramus at P ₄		93	86	55 ^a
Width of horizontal ramus at P ₄		35	39	17
Width of horizontal ramus at shallowest point along ramus	20	31	35	17
Minimum depth of horizontal ramus	50	76	87	53
Height, pterygoid process to coronoid process		157	145	83
Length of symphysis	135	184	135	70
Minimum width of symphysis	45	58	61	29
Greatest width of condyle	58	75	75	

^aEstimate on broken feature.



Figure 5. *Valenictus chulavistensis*, new species, SDSNH 36786, holotype left humerus. A, anterior view (stereophotographs); B, lateral view (stereophotographs); C, posterior view. Scale bar, 5 cm.

The proximal end of the humerus of *V. chulavistensis* is characterized by a relatively large and well-rounded capitulum (head) positioned only slightly below a thickened greater tuberosity. In *V. imperialensis*, *O. rosmarus*, and a humerus (USNM 187328) referred by Repenning and Tedford (1977: pl. 17) to the problematic odobenid *Pliopedia pacifica*, the greater tuberosity is also low relative to the head. In *V. imperialensis* the head is relatively larger than in the new species. The lesser tuberosity of both taxa is distinctly thickened and, with the greater tuberosity, encloses a narrow and proximally inset bicipital groove. The lesser tuberosity is positioned only slightly below the proximal capitulum. In *Odobenus* the lesser tuberosity is relatively smaller and placed more distally and the bicipital groove is broader and less inset. In the transverse plane, the greater tuberosity of both species of *Valenictus* is distinctly elongated, deflected medially, and of nearly

constant width to its anterior extremity. This medial deflection of the lesser tuberosity provides the proximal end of the humerus with a very broad profile in anterior aspect. This feature also characterizes the humeri of *V. imperialensis* and *Pliopedia pacifica* (USNM 187328).

The pectoral crest of the humerus of *V. chulavistensis* is elongate, like that of *Odobenus*, and extends as a broad ridge distally almost to the trochlea. By contrast, in *Imagotaria*, *Gomphotaria*, and *Aivikus*, the pectoral crest is strongly developed as a keeled ridge. In *Valenictus*, *Odobenus*, *Alachtherium*, and *Pliopedia* the pectoral crest gradually joins with the anterodistal surface of the humerus. In *Aivikus* and *Gomphotaria*, the pectoral crest displays an abrupt distal deflection and descends sharply to the anterodistal surface of the humerus. The deltoid tuberosity in *V. chulavistensis* is separate from the pectoral crest and positioned posterolateral to the

TABLE 5. Measurements of humeri of fossil odobenids (in mm).

	<i>Valenictus chulavistensis</i>					<i>Valenictus imperialiensis</i>	<i>Dusignathus seftoni</i>
	SDSNH 36786 ^a	SDSNH 38312	SDSNH 38315	SDSNH 35275	SDSNH 38300	LACM (CIT) 3926 ^a	SDSNH 43873
Greatest length, greater tuberosity to radial capitulum	326	315	306	263	300	253	346
Length, proximal capitulum to radial capitulum	325	306	310	270	296	252	321
Length, lesser tuberosity to radial capitulum	313	300	396	254	288	245	295
Transverse width across tuberosities	120	120	119	109	112	102	96
Greatest transverse width of proximal capitulum	91	88	85	77	79	69	86
Transverse width at narrowest part of shaft	56	55	56	61	63	51	62
Anteroposterior width at midshaft	75	94	86	76 ^b	74 ^b	88	97
Greatest width across epicondyles	162	159	168	137	153	125	
Greatest anteroposterior diameter of medial edge of trochlea	58 ^b	68	61	60	59	53	65
Greatest anteroposterior diameter of radial capitulum	50 ^b	52	42	52	46	39	
Greatest width of distal articulation	84	74	74	68	85	67	75 ^b
Transverse width of entepicondyle	53	50	63	38	59	47	34

^aHolotype.^bEstimate on broken feature.

crest on the lateral surface of a convex shaft. This configuration is like that of *Odobenus*, *V. imperialiensis*, and *Pliopedia* (USNM 187328) and unlike that of *Imagotaria*, *Gomphotaria*, *Pontolis*, and otariids, in which the insertion for the deltoid muscle appears as a ridge confluent with the pectoral crest. An intermediate condition is seen on humeri of *Alachtherium cretisi* (van Beneden 1877: pl. 3, fig. 1) and *Prorosmarus alleni* (MCZ 7713 in Repenning and Tedford 1977), in which, the deltoid insertion, although still on the pectoral crest, is more posterolaterally placed (i.e., the crest is transversely broadened).

The distal end of the humerus of both species of *Valenictus* is very broad, primarily because of the greatly enlarged entepicondyle. In the holotype of *V. chulavistensis* the width of the entepicondyle is 16% of the total length of the humerus. This measure varies from 14 to 20% ($N = 4$) in the referred humeri. A least-squares regression analysis revealed no significant correlation between enlargement of the entepicondyle and body size ($R^2 = 0.31$, $p > 0.05$). In *V. imperialiensis*, the entepicondyle falls within the range of *V. chulavistensis* at 19% of the total humeral length. In *Odobenus* the measure is only 8%, in *Alachtherium* about 8%, and in *Imagotaria* approximately 10%. In *V. chulavistensis*, the entepicondyle is extremely large and robust (Fig. 5C) and anteroposteriorly compressed with an outline roughly rectangular in both medial and anterior aspects. The proximodistal axis of this rectangular process is rotated posteriorly at its distal end. The entepicondyle of *V. imperialiensis* is also enlarged but more distally placed, rounded, and knoblike, rather than rectangular and rotated posteriorly. A partial humerus (USNM 13643) collected from the lower Pliocene San Joaquin Formation, Kettleman Hills, California, shares many features with humeri of *V. chulavistensis*, including the large and robust rectangular entepicondyle rotated posteriorly and the osteosclerotic internal bone structure. Repenning and Tedford (1977) illustrated this specimen (pl. 16, fig. 7) and referred it to *V. imperialiensis*. From the features discussed above, however, I tentatively refer USNM 13643 to the new species from Chula Vista.

The entepicondyle of *V. imperialiensis* is conspicuously reduced relative to the more enlarged condition in *V. chulavistensis*, *Odobenus*, and *Alachtherium*. The humerus of *Valenictus chulavistensis* also differs from that of *V. imperialiensis* in possessing a distinctly embayed olecranon fossa set medial to a distinctly

keeled supinator ridge. In *V. imperialiensis*, the olecranon fossa has a more convex surface adjacent to a broadly rounded supinator ridge. In fact, the entire posterior profile of the shaft of *V. imperialiensis* is planar, that of *V. chulavistensis*, sigmoidal.

As in all odobenids, the greatest anteroposterior diameter of the medial lip of the trochlea of *V. chulavistensis* is greater than that of the distal radial capitulum. However, the distal trochlear axis forms an angle of 90° ($N = 5$) with the humeral shaft's axis. In *V. imperialiensis* ($N = 1$) and *Alachtherium* ($N = 1$) this angle is 83°, while in *Odobenus* ($N = 2$) the angle is even more acute at 77°. This suggests that the antebrachium of the new species was not as medially directed as in *Odobenus*.

The important differences that distinguish the humerus of *V. chulavistensis* from that of *V. imperialiensis* include larger size, sigmoidal posterior profile, sharply keeled supinator ridge, robust and rectangular entepicondyle, more prominent ectepicondyle, and more obtuse angle between the shaft axis and distal trochlear axis.

Calcaneum.—The calcaneum of *V. chulavistensis* is unique. It is much broader distally than proximally. In *Odobenus* and *Imagotaria* (USNM 23862) these two dimensions are nearly equal. In dorsal or astragalus aspect (Fig. 6A), the sulcus calcanei between the sustentacular and ectal facets is broad and unlike the narrow sulcus of *Imagotaria* and *Odobenus*. Correlated with this broadening is a sustentacular facet that is positioned well distad, almost parallel with the distal cuboid facet. This distal placement of the sustentacular facet coupled with a well-developed lateral trochlear process (peroneal tubercle of Kellogg 1931) gives the calcaneum of *V. chulavistensis* its extremely broad distal end. The cuboid facet is an elongate rectangle, in contrast to the quadrate cuboid facet of *Odobenus* and the short rectangular cuboid facet of *Imagotaria downsii* (Repenning and Tedford 1977, USNM 23862). As in *Imagotaria* (USNM 23862), and in contrast to *Odobenus* and *Prorosmarus* (USNM 215236), the sustentaculum lacks a secondary shelf (Robinette and Stains 1970). The ectal facet is nearly planar, not convex as in *Odobenus*, *Imagotaria*, and otariids. The calcaneal tuber is long, with a prominent medial tuberosity (Fig. 6B) similar in size and form to that of *Odobenus* but less medially elongated than that of *Imagotaria* (USNM 23862). The cuboid facet forms an angle of between 14° and 21° with the longitudinal calcaneal axis. In *Imagotaria* this measure is between

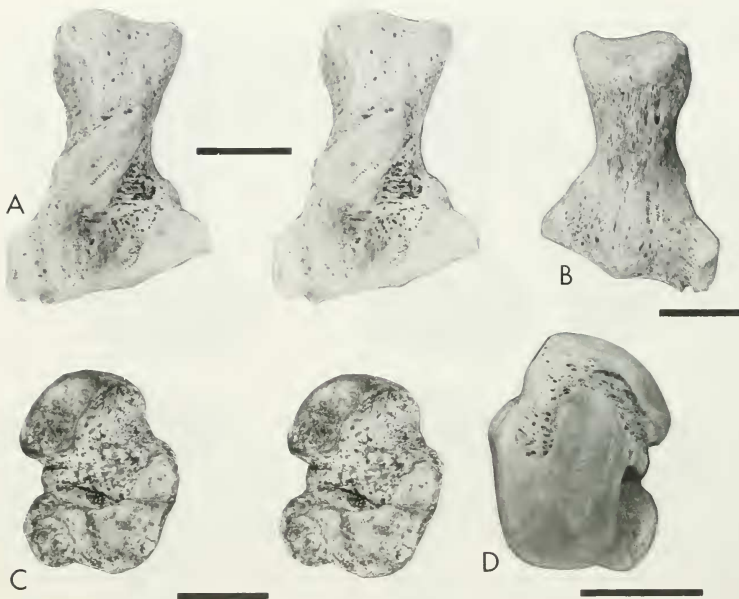


Figure 6. *Valenictus chulavistensis*, new species. A, B, SDSNH 36786, holotype right calcaneum. A, astragalus view (stereophotographs); B, palmar view. C, SDSNH 36786, holotype left astragalus, calcaneal view (stereophotographs). D, SDSNH 35273, referred left astragalus, proximal view. Scale bar, 5 cm.

10° and 15° , while in *Odobenus* it is between 30° and 35° . Like other skeletal elements, the calcaneum is constructed of osteosclerotic bone.

Astragalus.—This element also has an extremely unusual morphology (Figs. 6C, D). The capitulum is *not* set off from the stocky trochlear portion of the astragalus by a distinct neck as is in all other pinnipeds. The medial trochlear ridge (maleolar tibial facet) is distinctly longer than the lateral trochlear ridge (trochlear tibial facet), not shorter or of equal length as in *Odobenus* and *Imagotaria* (USNM 23867). In fact, the medial trochlear ridge extends so far proximally that it meets the medial plantar tuberosity. In *Odobenus* and *Imagotaria* both tibial articular trochlea are well separated from the medial plantar tuberosity by a distinct sulcus for the flexor hallucis longus tendon. In *V. chulavistensis*, the medial side of the medial trochlear ridge has a well-developed sulcus and there is no prominent lateral process (collum tali), only a flexure in the lateral outline of the astragalus (Fig. 6C). In *Odobenus* and otariids the lateral process is prominent and well separated from the capitulum. The capitulum of *V. chulavistensis* is directed medially at an angle of approximately 40° to the long axis of the astragalus. In plantar aspect (Fig. 6C), the medial sustentacular facet is confluent with the

navicular facet, in sharp contrast to the distinct and well-separated navicular and sustentacular facets of other pinnipeds. In *V. chulavistensis*, the region between the sustentacular and ectal facets is a very broad sulcus calcanei, correlated with the corresponding broad sulcus of the calcaneum. The ectal facet is broadly J-shaped and extends laterally to meet the plantar border of the vertical fibular facet (i.e., there is no proximolateral shelf between the ectal facet and the fibular facet as is seen in other pinnipeds). As in all odobenids, the astragalus of *V. chulavistensis* has a postero-medial calcaneal process (medial plantar tuberosity); however, the process in this taxon is a broadly rounded structure, less distinct than the prominent process of *Imagotaria*, as discussed by Repenning and Tedford (1977).

Phylogenetic relationships.—*Valenictus chulavistensis* is an odobene walrus closely related to modern *Odobenus rosmarus* and the fossil walruses *Alacatherium cretisi*, *Prorosmarus alleni*, and *Pliopedia pacifica* (Fig. 7). Odobene synapomorphies (numbers refer to characters as discussed by Deméré 1994, this volume) supporting this relationship include (1) external narial opening elevated above incisive margin, (9) palate narrow and arched transversely and longitudinally, (10) hard palate elongated, (11) palatine

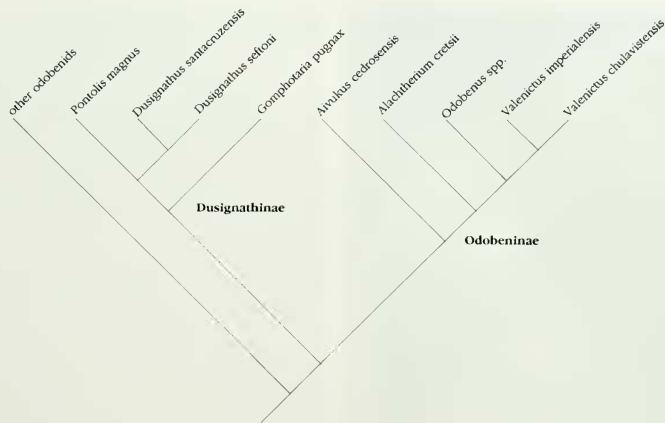


Figure 7. Phylogenetic relationships of dusignathine and odobenine walruses.

telescoped beneath alisphenoid, (12) hamular processes broad, (13) pterygoid strut lost, (17) mastoid processes as widest part of cranium, (19) cranial vertex with distinct flattened traction surface, (20) sagittal crest lost (also seen in some phocids), (21) zygomatic arches blunt and robust, (23) temporal fossae shortened, (24) optic foramen funnel-shaped, (25) orbital vacuity posteriorly placed, (29) upper canine with well-developed globular orthodontine column, (43) vesicular mandibular terminus, and (47) deltoid tubercle of humerus posterior to pectoral crest.

The humeri of *Alachtherium* and *Prorosmarus* possess features more plesiomorphic than those of *Odobenus* and *Valenictus*. Several autapomorphies of the new fossil species (e.g., edentulous lower jaw and nearly edentulous upper jaw, osteosclerotic long bones, and numerous features of the humerus, astragalus, and calcaneum) suggest that *V. chulavistensis* diverged from its common ancestor with *Odobenus* prior to pursuing its own unique evolutionary path toward its derived edentulous condition.

Recognition of *Valenictus chulavistensis* as a tusked odobenine walrus settles a long-standing question about the relationships of *Valenictus imperialensis*. When Mitchell (1961) first described this species he considered it to be a specialized odobenid. Later, he (Mitchell 1968) implied that *V. imperialensis* was distantly related to the Odobeninae. Repenning and Tedford (1977) and Barnes (1989) assigned this species to the Dusignathinae, with reservations.

Functional morphology.—A complete discussion of the functional aspects of the skeleton of *Valenictus chulavistensis* is beyond the scope of this report. Three aspects, however, are discussed here: development and function of elongated ever-growing canines (tusks), feeding behavior as it relates to tooth loss, and locomotor implications of the humerus.

Tusks and behavior.—Possession of homologous enlarged upper canines in *V. chulavistensis*, *Alachtherium*, *Odobenus*, and prob-

ably also *Prorosmarus* suggests that the common ancestor of these odobenine taxa had tusks and that modern *Odobenus* inherited them. In this light, adaptational scenarios explaining tusk evolution in *Odobenus* must also explain the development of tusks in all fossil walruses of temperate latitudes. The tusks of *Odobenus* must be considered not solely as adaptations for an arctic existence but as structures with a history. Fay (1982) showed that walruses do not use their tusks directly in benthic feeding, as erroneously suggested by other workers. The wear patterns noted by Fay (1982) on tusks of *Odobenus*, also preserved on tusks of *V. chulavistensis*, are the product of incidental abrasion during benthic feeding. As a walrus forages with its muzzle against the substrate, it drags its tusks passively through the bottom sediments, wearing their anterior margins. The anatomical and behavioral data of Fay (1982:137), when combined with the phylogenetic data presented here, suggest that tusks are not the product of viability selection but rather evolved for social display, most probably under the pressures of sexual selection. Walrus tusks, like cervid antlers, are structural adaptations for social interactions (e.g., intraspecific dominance) rather than as sea-floor "plowshares" or arctic "ice tongs." Presumably, *Valenictus chulavistensis* used its tusks for social display as does the living *Odobenus rosmarus*.

Jaws and feeding.—Possession of an edentulous lower jaw and nearly edentulous upper jaw begs the question, "how did *Valenictus chulavistensis* feed?" Fay (1982) has shown that modern walruses are suction-feeders, specializing on soft-bodied and thin-shelled benthic invertebrates (e.g., polychaetes, tunicates, and molluscs). According to Fay (1982) *Odobenus* does not use its peglike cheek teeth to crush prey but rather relies on a strong oral suction to ingest prey whole. He suggested that any function the cheek teeth retain is related to aquatic communication, supported by the observation that submerged walruses produce a loud clacking sound by percussive tooth occlusion. When feeding on thin-shelled pelecypods

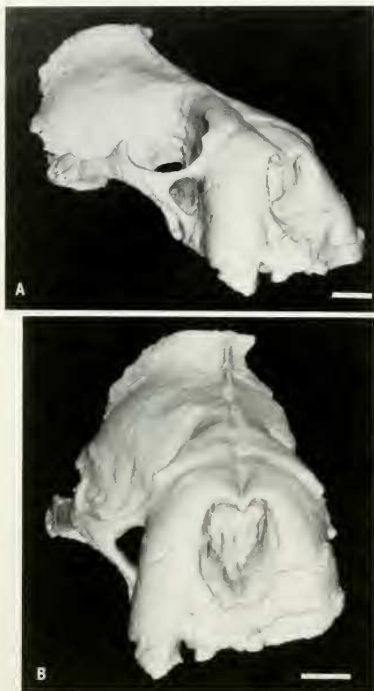


Figure 8. *Dasignathus seftoni*, new species, SDSNH 38342, holotype skull, computer tomography scan three-dimensional images. A, oblique lateral view; B, oblique anterior view. Scale bar, 3 cm.

Odobenus rosmarus sucks the mollusks from their shells before ingesting them (i.e., shells are not crushed by the teeth) (Fay 1982). With a strategy of feeding by oral suction, teeth are vestigial, implying that their loss in *V. chulavistensis* is not a "preadaptation" for starvation but a derived condition related to a unique feeding strategy. A test of this hypothesis is provided by the bearded seal, *Erignathus barbatus*, which as a strong suction-feeder and part-time benthic browser, frequently loses its teeth in old age (F. H. Fay, pers. comm.). In addition, the living monodontid, *Monodon monoceros*, and ziphiid odontocetes (e.g., *Mesoplodon* spp.) have lost all postcanine teeth and are oral-suction feeders, specializing on squid and small schooling fishes. Thus tooth loss following adoption of suction feeding is a derived condition at which several different groups of suction-feeding marine mammals have arrived independently. Since the common ancestor of *V. chulavistensis* and *Odobenus rosmarus* obviously had postcanine teeth, the edentulous

condition of *V. chulavistensis* is more derived than the retention of teeth by *Odobenus* and represents the first case among pinnipeds of loss of all teeth but tusks.

Humerus and locomotion.—The humerus of *V. chulavistensis* preserves an interesting mosaic of characters. Most conspicuous is the overall stockiness of the humerus and the greatly enlarged entepicondyle. Enlargement of the entepicondyle is correlated with an increase in the mass of the forelimb's flexor and pronator musculature (English 1980) and suggests that *V. chulavistensis* relied more on forelimb flexion and pronation during swimming than does *Odobenus*. As discussed by English (1980), however, the strong muscles suggested by the large entepicondyle might have served to oppose supination and passive forelimb extension rather than to impose pronation and flexion actively. This opposition to supination and extension are important actions in maintaining a rigid pectoral "rudder."

Gordon (1981) divided extant pinnipeds into three general groups by mode of aquatic locomotion: forelimb swimmers (i.e., otariids), hindlimb swimmers (i.e., phocids), and forelimb/hindlimb swimmers (i.e., odobenids). Forelimb-swimming otariids rely primarily on adduction and abduction of the forelimb rather than on flexion and extension (Howell 1929; English 1980; Gordon 1981), suggesting that pronation and supination are important muscle actions. Hindlimb-swimming phocids rely primarily on abduction and adduction of the hindlimb (Howell 1929). The forelimb/hindlimb swimming mode proposed for odobenids may be misleading, as walruses' primary source of aquatic propulsion is supplied by the hindlimbs; they use the forelimbs only for steering and stabilization (F. H. Fay, pers. comm.).

Berta and Ray (1990) suggested that forelimb/hindlimb aquatic locomotion is the primitive condition for pinnipeds, as presumed in *Enaliarctos*. Whether or not the condition in *Odobenus* is homologous with that in *Enaliarctos* requires further analysis. It does seem, however, that *V. chulavistensis* adopted a locomotor strategy involving more forelimb pronation, or suppression of pronation, than that of *Odobenus*. This implies a greater degree of forelimb involvement in aquatic locomotion in *Valenictus*.

Giffin (1992) independently assessed the swimming behavior of *Valenictus chulavistensis*, including 10 vertebrae from the holotype, in her analysis of pinniped locomotion. Assuming a correlation between neural canal anatomy and locomotor ability, she concluded that *V. chulavistensis* was a forelimb/hindlimb (hindlimb-dominated) swimmer like modern *Odobenus* and not primarily a forelimb swimmer like modern otariids. Importantly, Giffin found a close similarity between *Odobenus* and phocids in terms of axial innervation and correlated muscle activity.

The humerus of *Alachtherium*, like that of *Odobenus*, does not have an enlarged entepicondyle (van Beneden 1877: pl. 3, fig. 1), suggesting that the condition in *Valenictus* is uniquely derived, while that of *Odobenus* is a shared primitive feature retained from the common ancestor of all tusked odobenines.

The osteosclerotic nature of the limb bones of *V. chulavistensis* is unique among known fossil and living pinnipeds and is convergent with the condition in sirenians. Functionally, this may have reduced buoyancy for the species' presumed benthic feeding in temperate latitudes. The fact that *Odobenus rosmarus* lacks osteosclerotic bone is a puzzle but may be related to its arctic habitat of cold, dense bottom waters.

Discussion.—*Valenictus chulavistensis* is possibly the most completely known fossil odobenine, represented by essentially every major skeletal element. This species was relatively large, similar in overall size to modern *Odobenus rosmarus*, but smaller than the great fossil walrus *Alachtherium cretsii* from the early Pliocene of the eastern North Atlantic.

The genus *Valenictus* has long been considered a problematic taxon, in large part because the type species is based on a single

postcranial element not readily comparable with other more completely known taxa. Referral of the new San Diego Formation species to this genus offers a solution to this taxonomic problem by supplying important new information that confirms the odobenine relationships of *Valenictus*.

Valenictus imperialensis is also unusual because it occurs in the Imperial Formation of the Colorado Desert, Imperial County, California. The Imperial Formation was deposited during the late Miocene and early Pliocene in the proto-Gulf of California. As now, the Gulf had no direct connection with the temperate eastern North Pacific but instead extended south into tropical latitudes along a tectonic lineament characterized by crustal thinning and extension (Mammerickx and Klitgord 1982). The occurrence of tropical and subtropical molluscan taxa in the Imperial Formation, some with Caribbean affinities (Kew 1914; Vaughan 1917; Hanna 1926; Schremp 1981; Kidwell 1988), and their total absence in the well-studied marine Neogene deposits of coastal southern California, supports a strictly tropical connection and also implies an equatorial connection between the Caribbean and eastern tropical Pacific before the raising of the Isthmus of Panama. The invertebrate and vertebrate faunas of the proto-Gulf and temperate eastern Pacific were rather isolated from each other, implying a certain degree of endemism for the Imperial Formation faunas. Thus *V. imperialensis*, possibly confined to the subtropical proto-Gulf of California, may have been the result of late Miocene allopatric speciation. Furthermore, *V. chulavistensis* may represent a secondary late Pliocene dispersal of this clade into the temperate eastern North Pacific following emergence of the Isthmus of Panama.

The holotype humerus and only known specimen of *Valenictus imperialensis* shares several apomorphies with the humerus of *V. chulavistensis*. Although the possibility that the two species are conspecific cannot be ruled out altogether, the morphological differences presented above coupled with the late Miocene age of *V. imperialensis* and its apparent restriction to the proto-Gulf of California suggest that synonymy is unlikely. If all of the features shared by the two taxa represent synapomorphies inherited from a common ancestor and the additional apomorphies of *V. chulavistensis* represent uniquely derived features, *V. imperialensis* may not be diagnosable at the species level (i.e., it may represent a *nomen dubium*). This is a problem inherent in the questionable practice of describing fossil taxa from isolated skeletal elements of dubious diagnostic value. The discovery of additional material of *Valenictus imperialensis* and/or new material of other related odobenine species with the same synapomorphic features will help to resolve these questions.

Subfamily Dusignathinae Mitchell, 1968

Dusignathus Kellogg, 1927

Type species.—*Dusignathus santacruzensis* Kellogg, 1927.

Distribution.—Late Miocene and late Pliocene of California and Baja California.

Included species.—*D. santacruzensis* Kellogg, 1927, and *D. seftoni*, n. sp.

Emended diagnosis.—Dusignathine walruses distinguished from other taxa by the following apomorphies: mandibular symphysis narrowly V-shaped in occlusal aspect, lower canines closely appressed to each other, left and right dentaries forming acute angle of 60° at symphysis, rostrum shortened, and mandibular rami deep (relative to *Gomphotaria*).

Dusignathus seftoni n. sp.

Figures 8–11

Diagnosis.—A species of *Dusignathus* distinguished from *D. santacruzensis* by the following autapomorphies: upper and lower

cheek teeth forming a laterally convex arch in occlusal aspect, postcanine teeth in upper and lower jaws with medially rotated anteroposterior axes of roots, roots of all cheek teeth closely appressed, and dentary with deeply excavated masseteric fossa. Shares the following apomorphies with other designathines: nasal/frontal suture posteriorly directed and V-shaped; upper and lower canines enlarged as tusks.

Type material.—SDSNH 38342, a skull lacking the basicranium. Collected by Richard A. Cerutti and Matthew W. Colbert, 12 May 1989.

Etymology.—The species is named in honor of Thomas W. Sefton, who has generously supported the collection and study of fossil marine mammals from San Diego County.

Type locality.—SDSNH locality 3468, city of Chula Vista, San Diego County, California.

Horizon and age.—San Diego Formation, "lower member" of Deméré (1983), late Pliocene (Blancan NALMA correlative).

Referred specimens.—SDSNH 20801, right dentary preserving part of the symphyseal region of the left dentary; SDSNH 38256, damaged left humerus; SDSNH 43873, left humerus (all collected from the San Diego Formation). Complete locality information is available to interested researchers upon request.

Cranium.—The holotype cranium was damaged by earth-moving equipment. The left side of the braincase is missing, as is the left zygomatic arch. Also missing is the entire basicranium, including both auditory regions, mastoids, and postglenoid fossae. The majority of the occipital shield, including the paramastoid processes, is also missing. Anteriorly, the left tooth row is obliterated, and with it the posterior border of the palate and internal narial opening. The right I¹, C¹, and P¹⁻² are sheared off just distad of the alveoli. The pattern of suture closure (see Sivertson 1954) indicates a subadult individual.

The cranium (Figs. 8, 9, 10A, B) preserves many general features characteristic of odobenids, including a low sagittal crest (as in *Neotherium* and *Imagotaria*), lack of supraorbital processes of frontals (as in *Neotherium*, *Imagotaria*, *Gomphotaria*, cf. *Pontolis*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*), prominent antorbital processes (as in *Imagotaria*, *Gomphotaria*, *Pontolis*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*), and enlarged infraorbital foramen (as in *Imagotaria*, *Pontolis*, *Gomphotaria*, *Aivukus*, *Alachtherium*, *Valenictus*, and *Odobenus*).

The rostrum is short and broad relative to that of *Gomphotaria* (Table 2) and houses a pair of enlarged canines (tusks). The inclination of the canine root in relation to a vertical transverse plane is 33°, which is more vertically inclined (Figs. 8A, B) than the canines of *Gomphotaria pugnax* and approaches the condition in tusked odobenines. The frontal/maxilla suture forms an acute angle (approximately 60°) with the sagittal plane of the skull and is continuous with the nasal/frontal suture (Fig. 10B). The antorbital processes are split by the frontal/maxilla suture and are thus constructed from both frontal and maxilla. The nasals project posteriorly to form a web between the frontals (as in *Gomphotaria* and *Pontolis*, USNM 314300) and, anteriorly, are roughly rectangular (Figs. 9A, 10B). Thin ascending processes of the premaxillae overlap the nasals along 68% of their lateral margins. The anterior narial opening is more vertically oriented than that of *Gomphotaria* and ends in a prominent nasal process of the premaxillae. The floor of the narial opening is only slightly elevated (25 mm) above the level of the incisive margin. In contrast to *D. santacruzensis*, the maxillae are swollen to accommodate the roots of the enlarged canines, but not to the extent that they obscure the infraorbital foramina when the skull is viewed in anterior aspect (Fig. 8B).

The maxillary root of the zygomatic arch is delicately constructed, with a very slender dorsal strut. The ventral strut is directed dorsolaterally, in contrast to the more horizontally directed struts seen in *Imagotaria* and *Gomphotaria*. The effect of this is to

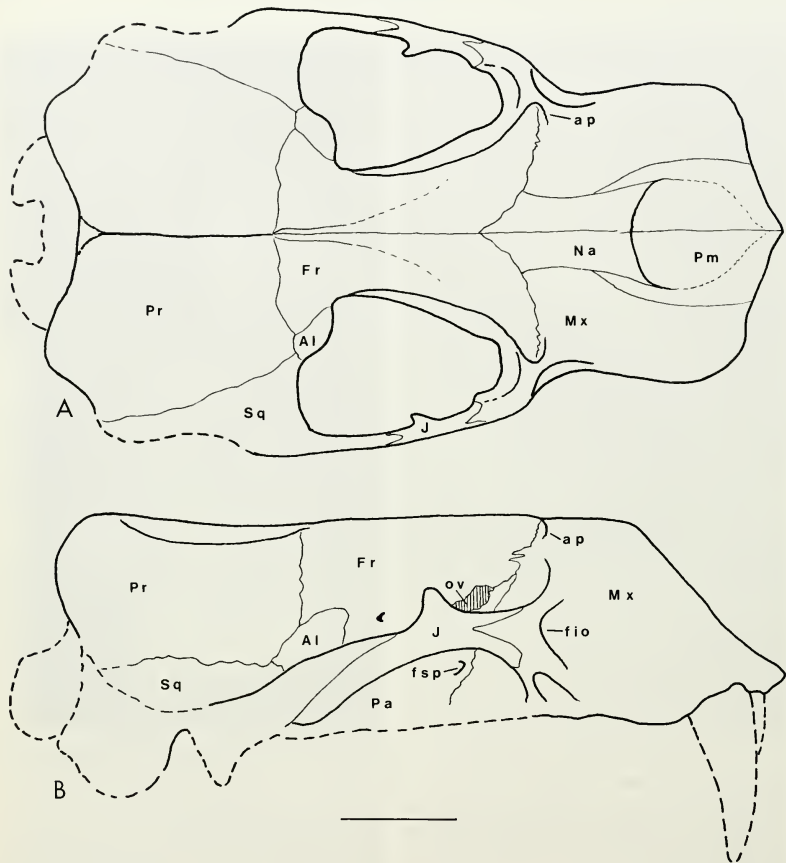


Figure 9. Reconstructions of *Dusignathus seftoni*, new species. A, dorsal view; B, lateral view. Al, alisphenoid; ap, antorbital process; fio, infraorbital foramen; fsp, sphenopalatine foramen; Fr, frontal; J, jugal; Mx, maxilla; Na, nasal; ov, orbital vacuity; Pa, palatine; Pr, parietal; Pm, premaxilla; Sq, squamosal. Scale bar, 5 cm.

give the infraorbital foramen a rounded triangular shape and a long axis inclined dorsolaterally, in contrast to *Imagotaria* and *Gomphotaria*, in which the long axis is directed horizontally. The ventral surface of the ventral strut is marked by a distinctive fossa (origin of the maxillo-naso-labialis muscle; Howell 1929) that is more prominent than that in *Aivukus*. The dorsal and ventral struts are positioned one above the other, in contrast to the condition seen

in *Gomphotaria*, whose the dorsal strut lies anterior to the ventral.

The jugal is also delicately constructed, and has a small triangular postorbital process (Fig. 8A). The orbit is large relative to that of *Gomphotaria*. The squamosal fossa forms a shelf over the missing external auditory meatus but is narrower than in *Gomphotaria*. The zygomatic portion of the squamosal is long and slender and forms a splintlike suture with the jugal.



Figure 10. *Dusignathus seftoni*, new species. A, B, SDSNH 38342, holotype skull. A, ventral view (stereophotographs); B, dorsal view. C, D, E, SDSNH 20801, referred right dentary. C, lateral view (stereophotographs); D, medial view; E, occlusal view (stereophotographs). Scale bar, 5 cm.

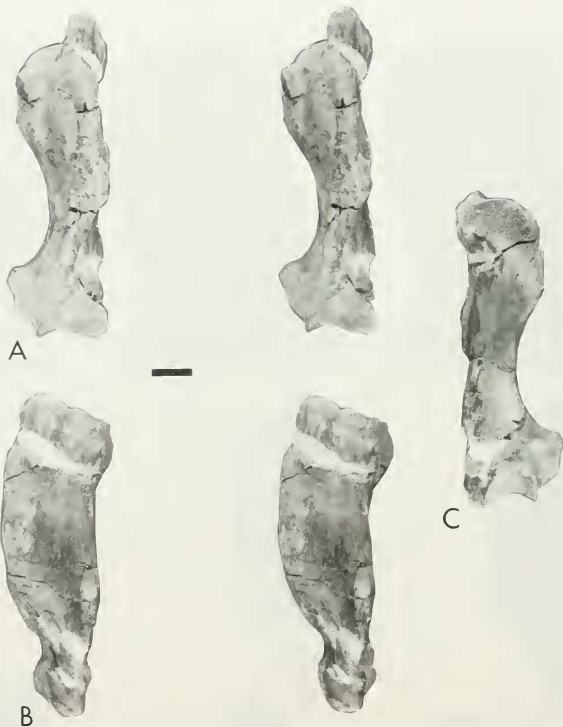


Figure 11. *Dusingnathus seftoni*, new species, SDSNH 43873, referred left humerus. A, anterior view (stereophotographs); B, lateral view (stereophotographs); C, posterior view. Scale bar, 5 cm.

The palate is broad and not obviously arched. A pair of large incisive foramina are positioned 15 mm posterior to the lateral incisors (Fig. 10A). The palatine foramina lie 30 mm anterior to the palatine/maxilla suture. The posterior border of the palate is not preserved.

The anterior margins of the frontals along the midline are elevated slightly above the level of the maxillae and nasals. This elevation is even more pronounced in *Gomphotaria*. The anterior portion of the interfrontal suture is slightly depressed and becomes obscured posteriorly in a fine median sulcus that continues posteriorly into the interparietal suture. Farther posterior the interparietal suture is marked by a low but distinct sagittal crest that merges posteriorly with the elevated right and left portions of the lambdoidal crest. The lambdoidal crest flares posteriorly, overhanging the largely missing occipital shield, which preserves no evidence of an occipital crista. The lateral walls of the braincase are

broadly convex (as in *Neotherium*, *Imagotaria*, *Alachtherium*, and *Odobenus*), not concave (as in *Pontolis* and *Gomphotaria*). The interorbital constriction is prominent and positioned posteriorly against the anterior border of the braincase.

The orbital wall, on the right side, preserves much of the frontal/maxilla suture as it descends from the antorbital process to meet the palatine where the suture bifurcates into the frontal/palatine and palatine/maxilla sutures. There is no lacrimal bone, and thus the maxilla forms the entire anterior border of the orbit. The frontal/palatine suture is present for a short distance anteriorly but is lost posteriorly in a narrowly elongated orbital vacuity. A thin plate of palatine separates the orbital vacuity from the maxilla and thus the palatine/maxilla suture has a broad exposure on the orbital wall as it descends to the sphenopalatine foramen. From here the suture continues ventrally to the broken palatal margin. The orbito-sphenoid is difficult to interpret because of breakage but seems to

extend posteriorly from the posterior border of the orbital vacuity to the alisphenoid. The dorsal border of the orbitosphenoid is marked by a distinct ethmoidal foramen. A large arcuate opening marks the region of the missing optic foramen and orbital fissure. The dorsal portion of the alisphenoid is well preserved and broadly exposed on the anterolateral border of the braincase. The parietal/squamosal suture is well preserved and runs horizontally from the enlarged alisphenoid back to the broken lambdoidal crest. The pterygoids are not preserved.

Within the brain case, the cribriform plate is preserved as a teardrop-shaped structure, widest ventrally. A portion of the bony tentorium is preserved on the right side of the braincase, and has no expression externally.

Upper dentition.—Only the intra-alveolar portions of six teeth (right and left C^1 , right and left I^1 , P^{1-2}) are preserved in the holotype cranium. The empty alveoli of I^2 , P^{3-4} , and M^{1-2} indicate only single-rooted teeth. There is no I^1 alveolus. Alveolar diameters for the right upper dental arcade I^2 – M^2 are as follows (anteroposterior length/transverse width in mm): 11.8/6.7; 14/20; 22/29.5; 13/12.5; 11/11; 14/10; 10/9; 8/7.4; 8.4/6.4.

The lateral incisor has an oval cross-section, with the long axis of the cross-section directed somewhat transversely. The right I^1 preserves a thin (1 mm) outer cementum layer surrounding a dense orthodentine core. The right C^1 of the new species is greatly enlarged relative to P^1 and has a large open pulp cavity (visible in computerized tomography images), suggesting either immaturity or continuous growth. The cross-sectional shape of this tooth is oval proximally (intra-alveolar), becoming roughly triangular distally. The distal cross-section approximates a right triangle, with the right angle placed medially and the hypotenuse corresponding to the labial surface of the tooth (Fig. 10A). In the holotype of *D. santacruzensis*, C^1 is oval throughout and has a closed root. In the rostral fragment (UCR 15244) from the Almejas Formation, Baja California, referred to *D. santacruzensis* by Repenning and Tedford (1977:46), C^1 has an oval cross-section and is approximately equal in size (alveolar diameter) to P^1 . The canines of *D. seftoni* consist of a thin outer cementum layer and an inner massive orthodentine core, as in *Gomphotaria*. There is no evidence of a central globular orthodentine column as in the tusked odobenine walrus. No traces of enamel were observed on the narrow remnant of crown. The anterolateral surface of the canine has a single shallow longitudinal groove quite different from the regular longitudinal fluting seen in *Gomphotaria* (see Barnes and Raschke 1991) and the three or four shallow longitudinal grooves of *Odobenus* (see Ray 1960).

There are alveoli for six postcanine teeth. The alveolus for P^1 is a deep oval opening with the long axis of the cross-section rotated medially 36° to the sagittal plane. One wall of this alveolus is marked by a faint vertical ridge, presumably corresponding to an incipient bifid root. This alveolus extends at least 26 mm into the maxilla. The walls of this and all cheek-tooth alveoli continuously taper to the root, quite unlike the bulbous peglike roots of *Gomphotaria*. The alveolus for P^2 is also relatively deep (15 mm) but nearly circular in cross-section. Alveoli for M^{1-2} are shallow (6 and 4 mm, respectively) and also circular in cross-section. In occlusal aspect, the postcanine tooth row forms a broad, laterally convex arc aligning with P^2 . The canine is positioned slightly outside of this arc. I^1 lies somewhat medial to C^1 , not entirely anterior to it as in *Neotherium*, *Imagotaria*, and *Pontolis*. All of the postcanine alveoli are closely appressed to each other, with no intra-alveolar spaces. A conspicuous diastema 10 mm wide separates C^1 from I^1 . This incisor–canine diastema is too narrow to accommodate an enlarged C^1 , suggesting that the lower canine occluded with the upper lateral incisor as suggested for *D. santacruzensis* (see Repenning and Tedford (1977); both the holotype and the referred partial rostrum from the Almejas Formation, UCR 15244).

Dentary.—SDSNH 20801 is a complete right dentary (Table 4)

with empty alveoli for a reduced incisor (possibly I_3), enlarged canine, and five postcanine teeth (presumably P_1 – M_1). Although the specimen was damaged, a good cast of the specimen, made before the damage occurred, is available at the USNM.

The horizontal ramus is deep dorsoventrally (Fig. 10C) as in *D. santacruzensis* and thick transversely as in *Gomphotaria*. Two large mental foramina are located midway along the lateral surface of the dentary, one each below P_1 and P_2 . The anterior mental foramen is oriented dorsoanteriorly, while the larger and more posterior mental foramen is oriented dorsomedially. In *D. santacruzensis* there are also two mental foramina, one each below P_2 and P_3 . In medial aspect, the mandibular symphyseal surface is a narrow oval (as in *D. santacruzensis* and *Pontolis*, USNM 335563) and not a broad oval (as in *Gomphotaria*). A portion of the medial wall of the left canine alveolus is preserved indicating a fused symphysis. The posteroventral portion of the symphysis is marked by a large globular and deeply excavated genial tuberosity, which contrasts with the more slender, ridgelike tuberosity of *D. santacruzensis*. The coronoid process is large and rises at an angle of about 55° from the tooth row. In *Gomphotaria* and *Pontolis* (USNM 335563) the coronoid rises at a shallower angle (40° and 35° , respectively). The masseteric fossa in *D. seftoni* is more deeply excavated than in any living or fossil odobenine. The fossa is divided into upper and lower portions by a conspicuous horizontal masseteric ridge. The base of the fossa is marked anteriorly by a deep depression that is continuous posteriorly with a sharply margined shelf that extends as a horizontal surface to the mandibular condyle. A similar sharply margined masseteric shelf was described for a gigantic proximal mandibular fragment (UCR 15245) collected from the Almejas Formation and questionably referred to *D. santacruzensis* by Repenning and Tedford (1977:47). The mandibular condyle of UCR 15245 measures 107 mm in width; that of SDSNH 20801, 75 mm. The condyle of *D. seftoni* is broad, slender, and spindle-like.

As mentioned, the symphysis is fused, and preserves a portion of the medial wall of the left canine alveolus. The region between the two lower canines is narrow and in occlusal aspect is shaped like an isosceles triangle, with the most acute angle pointing forward. The medial walls of the right and left canine alveoli come to within 20 mm of each other, leaving no area for dorsally placed incisors. Although badly damaged, a small alveolus for an incisor is closely appressed to the anterior border of the canine. This alveolus, best seen on the USNM cast, is approximately 38 mm below the canine alveolar margin. The canine alveolus is large and deep and extends to a point below the alveolus for P_2 . The canine's root (as determined from the alveolus) has an oval cross-section. The alveolar portion of the horizontal ramus in occlusal aspect is broad and laterally convex. The lingual borders of the cheek-tooth alveoli are higher than those on the labial border.

The pterygoid process (angular process) is large and projects medially approximately 20 mm as a hooklike flange as far as the medial border of the mandibular condyle. Anterior to this process, in lateral aspect, the ventral border of the ramus makes an abrupt flexure at the level of the distinct marginal process (Davis 1964). The marginal process itself is laterally swollen and rugose, marking the insertion for the digastric muscle. The marginal process on the type right dentary of *D. santacruzensis* is slender and not enlarged. In lateral aspect, the ventral border of the ramus, between the marginal process and the globular genial tuberosity, is broadly sigmoidal, as in *D. santacruzensis*.

The medial surface of the coronoid process is marked by a distinct and curving strutlike ridge that is inset from, but parallel to, the anterior coronoid crest.

Lower dentition.—Although no teeth are present in the referred dentary, the alveoli are well preserved. Postcanine alveoli 1–4 (presumably P_{1-4}) are transversely elongate ovals at the level of the tooth row. In *Dustignathus santacruzensis* P_1 has a circular alveolus,

while P_2-M_1 are elongated ovals. In *D. seftoni* the cross-sectional alveolar diameters for P_{1-4} (length/width in mm) are as follows: 23/19; 28/19; 29/22; 21/16. The conical alveolus for M_1 is circular at the level of the tooth row (13 mm diameter). The canine alveolus measures 48 by 34 mm. Alveolar depths for C_1-M_1 are as follows: 109 mm; 48 mm; 51 mm; 51 mm; 40 mm; 26 mm, respectively. Morphological details of the canine alveolus suggest that the root was open and had shallow widely spaced longitudinal grooves. Preserved on the alveolar walls of P_{1-4} are delicate vertical septa suggestive of vestigially bifid roots. In occlusal aspect, the entire tooth row (canine through M_1) forms a laterally convex arch.

Perhaps the most unusual feature of the lower tooth row is the orientation of the alveoli in occlusal aspect, specifically the angle made between the greatest cross-sectional dimension of the alveolus and a parasagittal plane. From back to front the roots undergo a progressive torsion, which in the right dentary is expressed as a successive counterclockwise rotation of the greatest cross-sectional dimension relative to a parasagittal plane: P_4 has rotated 52°, P_3 67°, P_2 96°, and P_1 130° (Fig. 10E).

Referral of the dentary (SDSNH 20801) to this new species is made on the basis of the comparably shortened tooth rows, laterally convex arching of the tooth rows, rotation of alveoli, and large size, features also observed in the holotype cranium.

Humerus.—A nearly complete left humerus (SDSNH 43873) and a partial left humerus (SDSNH 38256) are here referred to the new taxon (Fig. 11). SDSNH 38256 consists of the diaphysis and distal epiphysis, with the proximal epiphysis (including the capitulum and tuberosities) missing. SDSNH 43873 is complete except for damage to the proximal end (lateral one-third of the capitulum missing) and distal end (ectepicondyle missing). The following description relies primarily on features visible on SDSNH 43873.

The shaft is slender and similar in form to the humerus (USNM 23870) referred by Repenning and Tedford (1977) to *Imagotaria downsi*. The slenderness of the shaft and its large size (Table 5) suggest similarity to *Gomphotaria pugnax* (see Barnes and Raschke 1991). In posterior aspect, the lateral outline of the shaft is nearly straight and the medial outline is broadly concave. This contrasts with the more acutely concave medial profile of the humerus (UCMP 65318) questionably referred to *Dusignathus santacruzensis* by Repenning and Tedford (1977). Gross comparisons between UCMP 65318, USNM 23870, and SDSNH 43873 suggest that the latter two (*Imagotaria downsi* and *Dusignathus seftoni*) are more similar to each other than either is to UCMP 65318 (cf. *Dusignathus santacruzensis*). It should be noted that the holotype of *D. santacruzensis* does not include a humerus and that UCMP 65318 was only tentatively referred to this taxon. Thus, the actual morphology of the humerus of *D. santacruzensis* remains uncertain. However, this is not the case for *Gomphotaria*, another dusignathine walrus.

As in *Gomphotaria*, the proximal end of the humerus of *D. seftoni* has a rounded capitulum (head) positioned distinctly below the slender greater tuberosity. In *Valenictus*, *Pliopedia* (USNM 187328), and cf. *D. santacruzensis* (UCMP 65318) the greater tuberosity and humeral head are nearly at the same level. The lesser tuberosity of *D. seftoni* is knoblike and positioned distinctly below the capitulum, in contrast to the condition in *Imagotaria* (USNM 23870), in which the lesser tuberosity is nearly at the same level as the head. In medial aspect, the lesser tuberosity is broadened distally, while in anterior aspect the tuberosity is narrower than in *Valenictus*, *Pliopedia*, and cf. *D. santacruzensis*. The bicapital groove is broad and U-shaped.

The insertion for the deltoideus muscle is elongate and positioned on the pectoral crest as in *Imagotaria*, cf. *D. santacruzensis*, *Gomphotaria*, and *Aivukus* and differs from the posterolaterally displaced and isolated deltoid tubercles of *Odobenus*, *Valenictus*, and *Pliopedia* (USNM 187328). The pectoral crest itself is a slender

and elongate keeled ridge that descends posteriorly, with some flexion, to join the distal surface of the shaft, as in *Imagotaria* (USNM 23870). This flexed posterior segment of the crest is intermediate in form between the gradually tapered crests of *Odobenus*, *Valenictus*, and *Pliopedia* (USNM 187328) and the abruptly flexed crests of *Aivukus* and *Gomphotaria*. As in all odobenids the distal portion of the pectoral crest is directed toward the medial lip of the trochlea, which is considerably broader than the radial capitulum. Distally, the trochlear surface makes an acute angle of about 76° with the shaft axis.

The ectepicondyle is small relative to that of *Valenictus*. It is shaped much as in *Imagotaria* (USNM 23870) (i.e., a medially flattened knob in anterior aspect), not being triangular as in *Pliopedia* (USNM 187328) and cf. *D. santacruzensis* (UCMP 65318). Internally, the shaft of the humerus of *D. seftoni* is composed of cancellous bone, not osteosclerotic bone as in *Valenictus*. At 346 mm, SDSNH 43873 is longer (greater tuberosity to radial capitulum) than either *Pliopedia pacifica* (USNM 187328, 306 mm) or cf. *Dusignathus santacruzensis* (UCMP 65318, 271.6 mm) (Repenning and Tedford 1977).

Assignment of SDSNH 43873 and SDSNH 38256 to *Dusignathus seftoni* is based in part on the largeness of the former, which is compatible in size with the large mandible also referred to this species (SDSNH 20801). In addition, the elevated greater tuberosity of *D. seftoni* and the flexed pectoral crest are distinctive features shared with another dusignathine, *Gomphotaria*. And finally, the overall generalized morphology of the referred humeri clearly separates them from humeri of the only other odobenid known from the San Diego Formation, *Valenictus chulavistensis*.

Phylogenetic relationships.—*Dusignathus seftoni* is a dusignathine closely related to the late Miocene walrus *D. santacruzensis* and *Gomphotaria pugnax*. Synapomorphies supporting this relationship (Fig. 7) include (3) posteriorly directed V-shaped nasal/ frontal suture, (32) upper and lower canines enlarged as tusks, and (45) dentary with sinuous ventral border (numbers refer to characters as discussed by Deméré 1994, this volume).

Referral of *D. seftoni* to *Dusignathus* is based largely on features of the lower jaw. These include the sharply divergent mandibular arch and presumed shortened rostrum, as well as the extremely deep horizontal ramus and unreduced closely appressed lower canines. In both species of *Dusignathus*, rostral shortening did not result in loss of cheek teeth. However, in *D. seftoni* the accommodation of the cheek teeth into a shortened tooth row involved rotation and close appression of the roots of individual teeth. In *D. santacruzensis* the lower postcanine teeth lack any indication of rotated roots. Although the possibility exists that root rotation is an ontogenetic feature, *D. seftoni* is distinguished by other characters, including C^1 with triangular cross-section, C_2 enlarged as a tusk, laterally convex upper and lower cheek-tooth rows, and larger size.

In *Dusignathus seftoni* as in *Gomphotaria pugnax*, pleiomorphic features such as a distinct sagittal crest, robust coronoid process, and large masseteric fossa imply a powerful jaw depressor musculature.

Discussion.—The genus *Dusignathus* is now known from two species, one from the late Miocene of central California and possibly Baja California and a second from the late Pliocene of southern California. *Dusignathus seftoni*, the geologically youngest known dusignathine walrus, clearly shows that members of this clade survived into late Pliocene time along the eastern North Pacific margin.

The holotype skull of *D. seftoni* is from a subadult individual, possibly a male, while the referred dentary and large humerus are from adult animals, almost certainly males. The dimensions of the dentary suggest that the new species was large, approaching modern *Odobenus*. Repenning and Tedford (1977) suggested that the type of *D. santacruzensis* was probably a female, so sexual dimor-

phism may account for some of the size discrepancy between the two species.

The shortened rostrum with steeply inclined tusks of *D. seftoni* is convergent with the condition in *Odobenus*. The size and cross-sectional shape of the upper and lower canines differ sufficiently from those of *D. santacrucensis* (the holotype and referred rostrum of Repenning and Tedford 1977:46, UCR 15244) to suggest that evolution of the San Diego species involved tusk development. The generalized morphology of the referred humeri suggests that this species, like *Imagotaria*, might have been more like otariids in its swimming habits than modern *Odobenus*. This is especially evident in the enlarged greater tuberosity, high and elongate pectoral crest, and relatively unenlarged entepicondyle. Repenning's (1976) suggestion that *Imagotaria* was a generalist neritic carnivore might apply equally to *Dusignathus seftoni*.

SUMMARY

The two new species of walruses described here increase our knowledge of odobenid evolution in many ways. *Valenictus chulavistensis* is possibly the most completely known fossil odobenine, represented by essentially every major skeletal element. This taxon preserves a reduced dentition previously unknown for marine carnivorans, emphasizing the morphological extremes possible in the marine realm. *Valenictus chulavistensis* clearly shows that possession of ever-growing tusklike upper canines is an inherited feature shared with the fossil *Alachtherium* and modern *Odobenus*. This realization, coupled with the observation that walruses do not use their tusks directly in benthic foraging, lends support to the hypothesis that walrus tusks evolved as social display structures, in a sense similar to the antlers of cervids. In addition, many other morphological features shared by *Odobenus*, *Alachtherium*, and *Valenictus* provide direct evidence for primitive character states near the base of the tusked odobenine clade.

Assignment of the new species to *Valenictus* clarifies the taxonomic and phylogenetic aspects of this formerly problematic taxon and provides a sense of the true taxonomic diversity of odobenine genera.

Dusignathus seftoni is the third described dusignathine species and illustrates the range of taxonomic diversity in this clade of double-tusked walruses. The shortened rostrum, with its condensed but complete dentition, parallels the condition in tusked odobenines but is associated with an unreduced temporal musculature.

Valenictus chulavistensis and *Dusignathus seftoni* were sympatric along the eastern North Pacific margin during the late Pliocene, approximately 2–3 Ma, illustrating the odobenids' past diversity. *V. chulavistensis* and *D. seftoni* may have avoided direct competition through resource partitioning, with the former specializing on benthic invertebrates and the latter remaining a generalist neritic fish and squid eater.

Extinction of the entire dusignathine clade must be viewed as a Pleistocene event, with only *Odobenus* of the odobenine clade surviving to the Recent. Recognition of *Valenictus chulavistensis* in Californian Tertiary deposits illustrates that tusked odobenines remained a part of the North Pacific pinniped fauna at least into the late Pliocene.

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